SANDAKANIA 9 (1997): 35–54

Viburnum clemensae (*Caprifoliaceae s.l.*), an unusual dioecious species from the high mountains of Sabah (Borneo)

C. Puff[1], R. Buchner[1] & J.B. Sugau[2]

[1]Institute of Botany, University of Vienna,
Rennweg 14, A-1030 Vienna, Austria

[2]Forest Research Centre, Sepilok,
P.O. Box 1407, 90715 Sandakan,
Sabah, Malaysia

Summary. The character states of *Viburnum clemensae*, a species endemic to Borneo and first known from the Mount Kinabalu area, were investigated. Of particular interest is the occurrence of dioecy (previously unrecorded for the genus and family). The small flowers are characterized by a (sub)rotate corolla and valvate lobes in the bud. Male flowers have a much reduced sterile gynoecium but a well-developed ovary roof nectary; the tricarpellate female flowers produce filaments but anthers are entirely absent. The inferior ovary of the female has one well-developed locule with a solitary ovule on a placenta that is much enlarged below; two aborted additional locules are discernible but neither aborted (vestigial) ovules nor vestigial archesporia were detected. The drupaceous fruits have deeply ruminate, solitary seeds with a characteristic longitudinal furrow on the abaxial side. A detailed account of the fruit and seed development and anatomy is included. The species has spheroidal, 3-colpate pollen with a reticulate exine. In the vegetative region, the presence of domatia on the lower leaf surface, of stipules and of stalked glands on the petioles are noteworthy. An evaluation of the data obtained suggests that *Viburnum clemensae* is a rather derived and unusual species whose generic position, nevertheless, is undisputed.

During an expedition to Trus Madi, whose main aim was to study, collect and preserve Rubiaceae (C.P.), we discovered a population of male and female plants of a species which we initially identified as a member of the coffee family. The decussately arranged entire

Fig. 1. *Viburnum clemensae*. Branch with male inflorescences; note domatia on lower leaf surface (arrows). From *Sugau et al.* JBS 137.

leaves with domatia, stipules, dioecy, panicle-like inflorescences, small sympetalous flowers with a rotate corolla and an inferior ovary, and drupes with a single ruminate seed were all in agreement with character states in that family.

Under the assumption that it was perhaps an ill-known or new Rubiaceae, we carried out a detailed investigation and, moreover, sent leaf samples to Prof. B. Bremer (Univ. Uppsala, Sweden) for DNA analysis. The study revealed that some of the data obtained did not "fit" Rubiaceae, and the DNA data indicated that the plants in question must belong to *Viburnum* (Caprifoliaceae *s.l.*).

A subsequent literature search and screening of the specimens in the SAN herbarium brought to light that the collected plants are *Viburnum clemensae* Kern (Fig. 1), an ill-known species, for which dioecy had not been recorded.

Material and Methods

Detailed anatomical, morphological and palynological investigations (Fig. 2–9) are based on samples preserved in FPA and FAA of the collections *Sugau et al.* JBS 134 (SAN, WU) (female), JBS 137 (SAN) (male), and *Puff* 950308-1/2 (WU, preserved samples only; female and male). See "Specimens examined" for details.

Methods used follow those given in Igersheim (1993).

Observations

Habit

A treelet or small tree, *c.* 2–11.5 m tall, with a bole *c.* 2.5–5 cm in diameter, and a wide, open crown (bole up to *c.* 10 m, and crown to 5 m in the largest individuals). Outer bark smooth or finely scaly, mottled, dark grey, brown or greenish-brown; inner bark brown to yellowish; wood yellowish pale brown, reddish-white or white.

Leaves and stipules

Leaves decussate and petiolate (petioles 10–25 mm long). Leaf blades oblong-lanceolate, 60–130 × 25–55 mm, narrowed to the base and acute to acuminate at the apex, glabrous, with entire margins. Venation brochidodromous, the veins (mid-rib with 3–5 pairs of primary lateral veins) prominently raised below.

The lower leaf surface bears pit domatia in the axils between mid-rib and primary lateral veins, and sometimes also between primary and secondary lateral veins; they are not present in every vein axil, but randomly distributed (often only a few per leaf). Kern (1951) and Kern & Steenis (1951) erroneously described this as "underside glandular-pitted"; Brouwer

& Clifford (1990) correctly listed the species as having pit domatia and, moreover, mentioned the occurrence of (pit, pocket and hair tuft) domatia in another 10 *Viburnum* species.

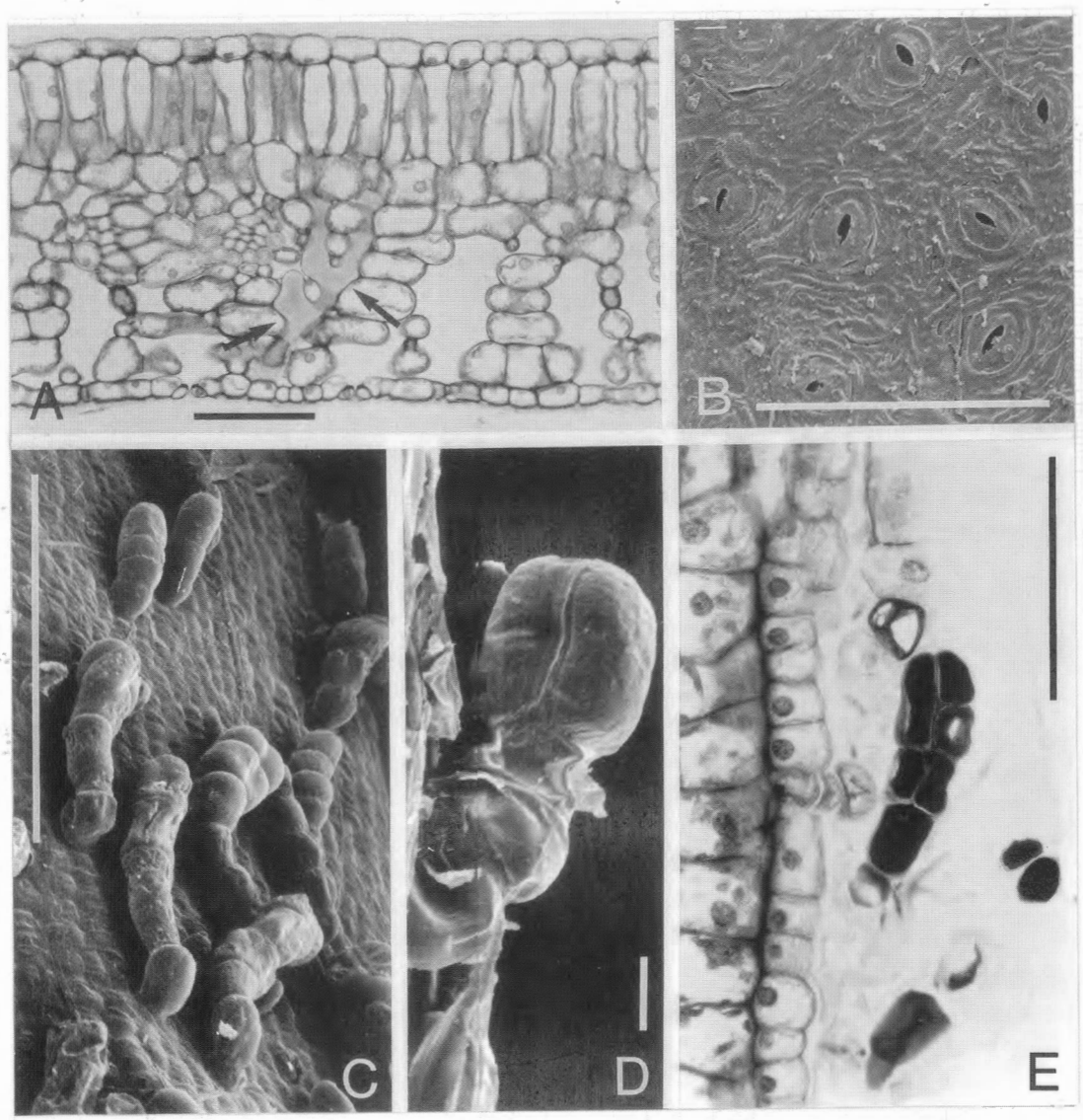


Fig. 2. Leaf anatomy, stomata and glandular hairs of *Viburnum clemensae*. **A**, Leaf blade section, note sclereids (arrows). **B**, view of lower leaf surface showing stomatal apparatus. **C–D**, glandular hairs on base of petiole (C) and pedicel (D). **E**, section of glandular hairs (from petiole). A, E, microtome sections; B–D, SE-micrographs. Scale bars: 0.1 mm (A; B; C; E); 10 µm (D).

Interpetiolar stipules, linear-lanceolate, *c.* 3.5 × 2 mm, are present. They, however, fall early and are usually only observable on the youngest parts of a shoot.

Stalked glands (multicellular hairs with a uniseriate stalk and a pluricellular glandular head) were observed on petioles (and also on pedicels, Fig. 2C–E, and on calyx lobes, Fig. 4E). Glandular hairs of basically the same structure have been previously recorded for *Viburnum* species (cf. Solereder 1899).

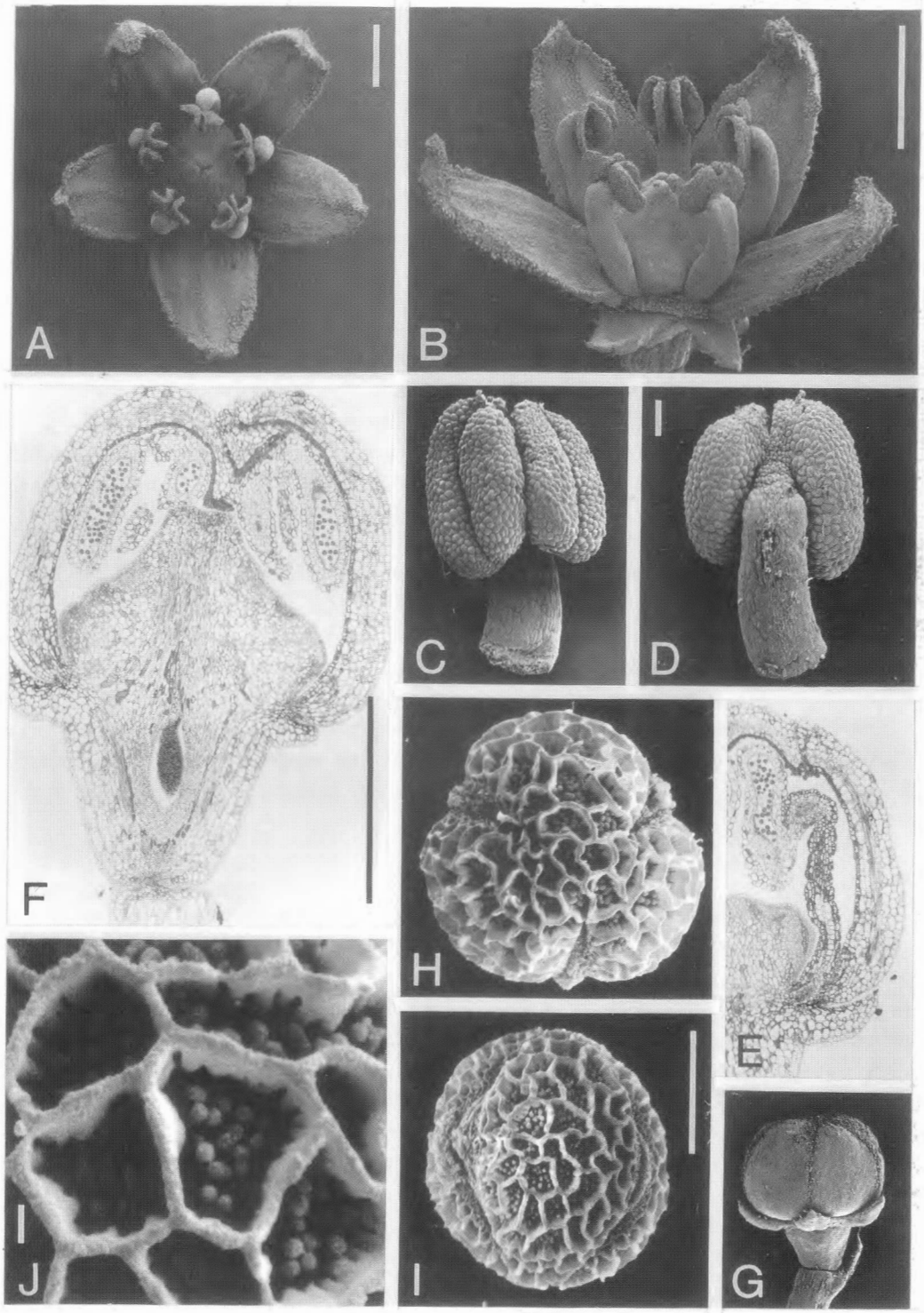
Leaf anatomy (Fig. 2A)
Below the upper epidermis (with cells larger than those of the lower epidermis) is a single layer of elongated palisade cells. The large-celled spongy mesophyll is loose and comprised of relatively large cells; occasional sclereids are present (Fig. 2A: arrows). The leaves are hypostomatic; the stomatal apparatus (cf. Fig. 2B) is of an "unspecialized" kind, i.e., the stomata are not surrounded by specially shaped and arranged companion cells but by irregular cells which are not different from the other epidermis cells (a general characteristic for the Caprifoliaceae, noted as early as 1899 by Solereder).

Inflorescences
The paniculate inflorescences are terminal, broadly to narrowly pyramidal in shape, and many- to several-flowered (Fig. 1). Inflorescences seem to exhibit a quite distinct sexual dimorphism. It appears to be the rule that male inflorescences are always more-flowered than in females. Whether there is also a marked difference in size could not be fully confirmed as inflorescences with open flowers were only available for males (80–110 mm long), whereas females either only had buds (inflorescences 10–22 mm long) or fruits at varying stages of maturity (much larger). Before and at anthesis, inflorescence axes (peduncles, pedicels) are filiform; in fruiting stage they not only elongate but also thicken somewhat.

Flowers
The flowers are unisexual (distributed on separate plants) and 5-merous (except for the tricarpellate gynoecium).

Calyx
The calyx is made up of 5 free, triangular lobes, *c.* 0.5–1 mm long. Calyx lobes of male flowers tend to be smaller than those of females (compare Fig. 3G and 4G). Both the calyx lobes (ab- and adaxial side and margins) and adjacent areas of the inferior ovary are beset with glandular hairs (Fig. 4E: arrows) which, however, are smaller than those on the vegetative parts of the plants.

Corolla
The yellowish-green, creamy to white corolla is (sub)rotate, i.e., characterized by the almost complete absence of a corolla tube (Fig. 3A–B, 4A). The corolla lobes are 1.5–2 mm long.


A
B
C
D
F
H
E
I
J
I
G

The aestivation of the corolla lobes in bud is essentially valvate (Fig. 3G, 4G), although microtome sections reveal that, near the base, some of the lobes show a trend towards imbricate aestivation (very indistinct overlaps of lobe margins). This observation is of some importance as *Viburnum* is characterized as being imbricate in bud (Kern 1951), and the Caprifoliaceae as a whole as "usually imbricate" (Zomlefer 1994). It seems plausible that the shift to valvate aestivation is linked with the very small flower size in *Viburnum clemensae*.

Androecium

The anthers of male flowers are introrse, dorsi-medifixed, broadly oblong to roundish and *c.* 0.5–0.8 mm long. The pollen sacs of each theca are slightly unequal in size (the outer being somewhat larger; Fig. 3C). Anthers open by means of two longitudinal slits (one per theca; Fig. 3A–B).

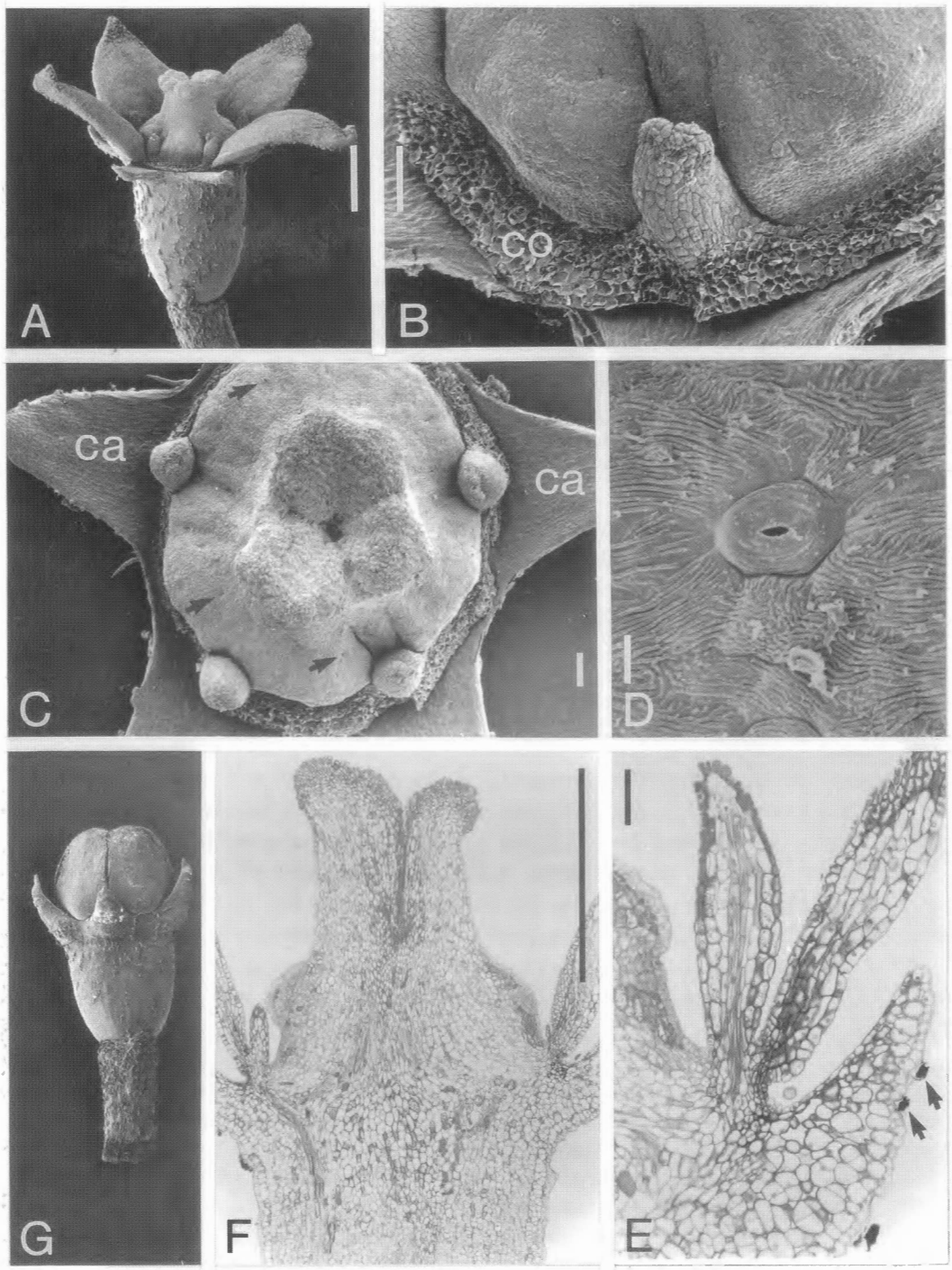
The filaments, to *c.* 1 mm long, are "hooked", i.e., differentiated into a long, lower portion and a short, round upper portion which is held at a right angle to the lower part (Fig. 3B, D, E). The lower filament portion is laterally compressed, so that it appears quite broad in the ventral and dorsal view of the stamens depicted in Fig. 3C–D. The filaments are inserted between the base of the corolla and the base of the disk (Fig. 3E).

In female flowers, the androecium is comprised of 5 staminodes with entirely reduced anthers but well-developed filaments (Fig. 4A–C, E–F) whose insertion is the same as in male flowers (Fig. 4E).

Gynoecium

The non-functional tricarpellate gynoecium of male flowers has a small and reduced, turbinate inferior ovary (Fig. 3G; compare with 4A, G). Longitudinal sections reveal that it has a central hollow in which there is a homogenous, dark-staining rod-like tissue (Fig. 3F). The latter is most probably the rudiments of the placenta and/or the infertile remnants of an ovule. Three rudimentary stigma lobes are recognizable, although smaller and less distinct than in female flowers (Fig. 3A–B; compare with 4A). As compared to female flowers, the stylar area is very indistinct (compare Fig. 3B and 4A, and also longitudinal sections, Fig. 3F and 4F); the large disk-nectary (= ovary roof nectary; see female flowers, below, for further details) gradually merges into the rudimentary style.

Fig. 3. *(opposite)* Male flower and pollen of *Viburnum clemensae*. **A–B**, flowers as seen from above and in side view. **C–D**, stamen in ad- and abaxial view. **E**, longitudinal section of stamen showing introrse, dorsi-medifixed anther on hooked filament (from bud). **F**, longitudinal section of bud showing rudimentary gynoecium and large ovary roof nectary. **G**, male bud, note valvate aestivation of corolla lobes and small, rudimentary ovary (compare with Fig. 4G). **H–J**, pollen; H, polar view; I, equatorial view; J, mesocolpium, note intraluminar bacula. A–D, G–J, SE-micrographs; E–F, microtome sections. Scale bars: 1 mm (A=G; B; E=F); 0.1 mm (C=D); 10µm (H=I); 1 µm (J).


A
B
co
ca
ca
C
D
G
F
E

The aestivation of the corolla lobes in bud is essentially valvate (Fig. 3G, 4G), although microtome sections reveal that, near the base, some of the lobes show a trend towards imbricate aestivation (very indistinct overlaps of lobe margins). This observation is of some importance as *Viburnum* is characterized as being imbricate in bud (Kern 1951), and the Caprifoliaceae as a whole as "usually imbricate" (Zomlefer 1994). It seems plausible that the shift to valvate aestivation is linked with the very small flower size in *Viburnum clemensae*.

Androecium

The anthers of male flowers are introrse, dorsi-medifixed, broadly oblong to roundish and *c.* 0.5–0.8 mm long. The pollen sacs of each theca are slightly unequal in size (the outer being somewhat larger; Fig. 3C). Anthers open by means of two longitudinal slits (one per theca; Fig. 3A–B).

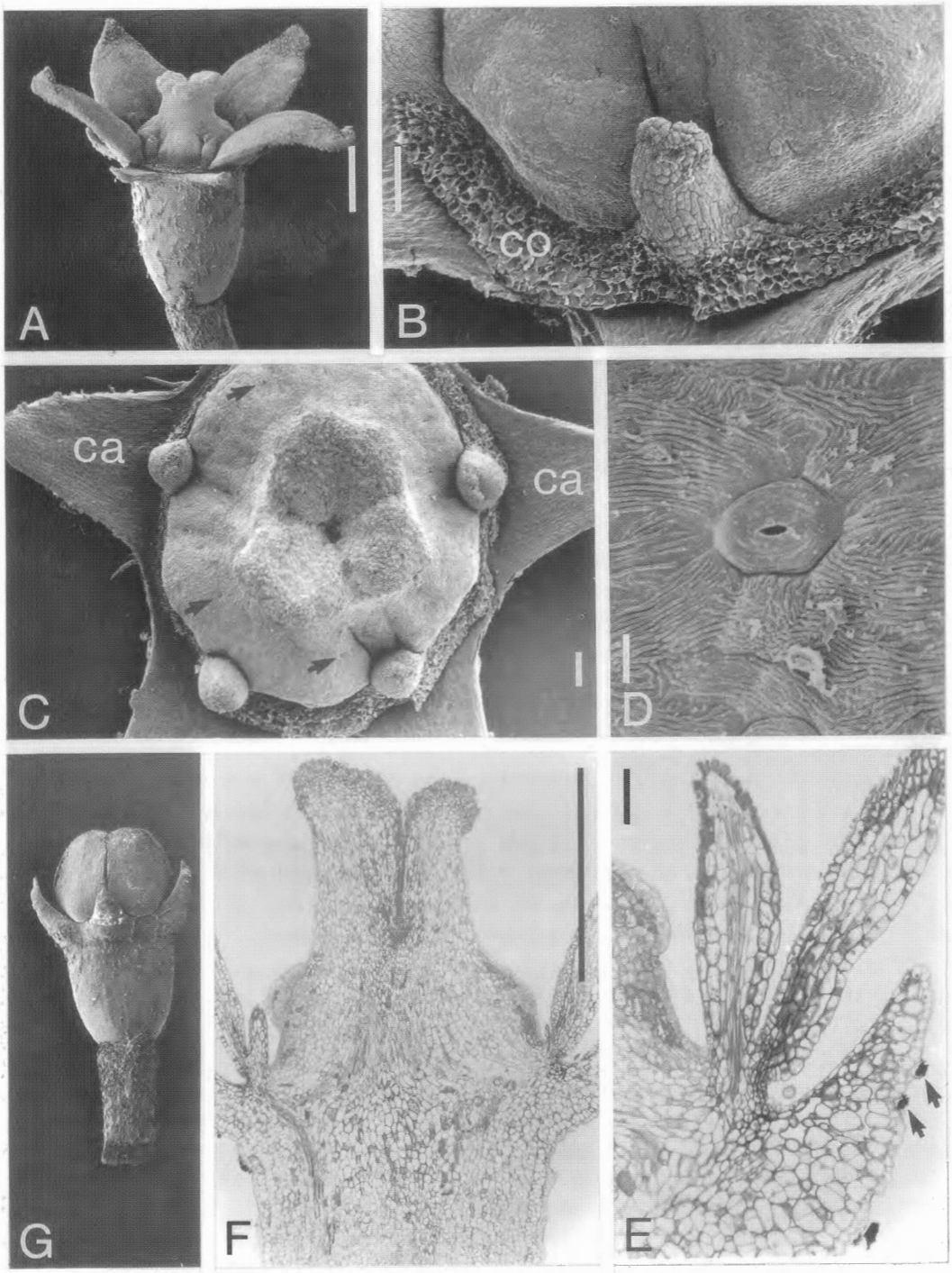
The filaments, to *c.* 1 mm long, are "hooked", i.e., differentiated into a long, lower portion and a short, round upper portion which is held at a right angle to the lower part (Fig. 3B, D, E). The lower filament portion is laterally compressed, so that it appears quite broad in the ventral and dorsal view of the stamens depicted in Fig. 3C–D. The filaments are inserted between the base of the corolla and the base of the disk (Fig. 3E).

In female flowers, the androecium is comprised of 5 staminodes with entirely reduced anthers but well-developed filaments (Fig. 4A–C, E–F) whose insertion is the same as in male flowers (Fig. 4E).

Gynoecium

The non-functional tricarpellate gynoecium of male flowers has a small and reduced, turbinate inferior ovary (Fig. 3G; compare with 4A, G). Longitudinal sections reveal that it has a central hollow in which there is a homogenous, dark-staining rod-like tissue (Fig. 3F). The latter is most probably the rudiments of the placenta and/or the infertile remnants of an ovule. Three rudimentary stigma lobes are recognizable, although smaller and less distinct than in female flowers (Fig. 3A–B; compare with 4A). As compared to female flowers, the stylar area is very indistinct (compare Fig. 3B and 4A, and also longitudinal sections, Fig. 3F and 4F); the large disk-nectary (= ovary roof nectary; see female flowers, below, for further details) gradually merges into the rudimentary style.

Fig. 3. *(opposite)* Male flower and pollen of *Viburnum clemensae*. **A–B**, flowers as seen from above and in side view. **C–D**, stamen in ad- and abaxial view. **E**, longitudinal section of stamen showing introrse, dorsi-medifixed anther on hooked filament (from bud). **F**, longitudinal section of bud showing rudimentary gynoecium and large ovary roof nectary. **G**, male bud, note valvate aestivation of corolla lobes and small, rudimentary ovary (compare with Fig. 4G). **H–J**, pollen; H, polar view; I, equatorial view; J, mesocolpium, note intraluminar bacula. A–D, G–J, SE-micrographs; E–F, microtome sections. Scale bars: 1 mm (A=G; B; E=F); 0.1 mm (C=D); 10µm (H=I); 1 µm (J).


A
B
co
C
ca
ca
D
G
F
E

Female flowers are characterized by an ovoidal inferior ovary, *c.* 1.5–2 mm high (Fig. 4A, G) and a 3-lobed stigma which is quite clearly demarcated from the common style (Fig. 4A, C, F). The stigma lobes are beset with receptive papillae on the adaxial side (Fig. 5A). The central hollow seen from above (Fig. 4C) indicates that the style is not completely fused (compare with sections, Fig. 4F, 5B).

A large, cone-like ovary roof nectary, indented in the region of the filaments, is present (Fig. 4A–C, F and 5C, the latter also showing the dark-staining nectar-producing tissue). Its surface has rather few, irregularly distributed, often somewhat sunken "nectar slits" (stomata-like openings) on its surface (Fig. 4C–D). Comparable disk nectaries with nectar slits have been observed in other *Viburnum* species (cf. Wagenitz & Laing 1984, Erbar 1994).

The anatomy of the ovary corresponds well with that of other *Viburnum* species studied (Wilkinson 1948: 14 spp., from all but two sections recognized in the genus). The ovary is clearly tricarpellate, as revealed by the 3-lobed stigma and style (Fig. 5A–B), and the clearly 3-partite style outline and 3 vascular bundles in the centre of the ovary roof nectary (Fig. 5C), but it has only a single well-developed locule with a solitary fertile ovule.

Sections from a level higher than the insertion point of the solitary fertile ovule clearly show the initiation of three locules, the one containing the fertile ovule already being larger than the other two (Fig. 5D). Lower down, the additional two gaps (aborted locules) gradually disappear. In none of the sectioned flowers were aborted (vestigial, sterile) ovules or vestigial archesporia detected in either these two locules or in the well-developed locule. As already noted by Wilkinson (1948), aborted ovules are not always present. One possibility is that *Viburnum clemensae* is such a derived species that they are no longer initiated.

Characteristic for the ovary is the conspicuous placenta that becomes much enlarged particularly below the fertile ovule, in this region filling out most of the space of the locule (Fig. 5G–H, 6A; note the small size of the ovule in relation to the placenta in the latter). Wilkinson (1948) found a comparable, enlarged placenta in *Viburnum sieboldii* (which is placed in the same section as *Viburnum clemensae*, namely sect. *Thyrsosma*; cf. Kern 1951).

Fig. 4. *(opposite)* Female flower of *Viburnum clemensae*. **A**, flower in side view (corolla lobe in front removed). **B**, staminode and portion of the disk (co, corolla; removed). **C**, stigma lobes, style, ovary roof nectary (arrows: nectar slits) and staminodes as seen from above (corolla removed; ca, calyx). **D**, stomata-like nectar slit on ovary roof nectary. **E**, longitudinal section of staminode, inserted between base of nectary (left) and base of corolla (right); note dark-stained glandular hairs (arrows) on the calyx. **F**, longitudinal section of stigma, style and ovary roof nectary. **G**, female bud, note valvate aestivation of corolla lobes and well-developed ovary (compare with Fig. 3G). A–D, G, SE-micrographs; E–F, microtome sections. Scale bars: 1 mm (A=G; F); 0.1 mm (B; C; E); 10 μm (D).

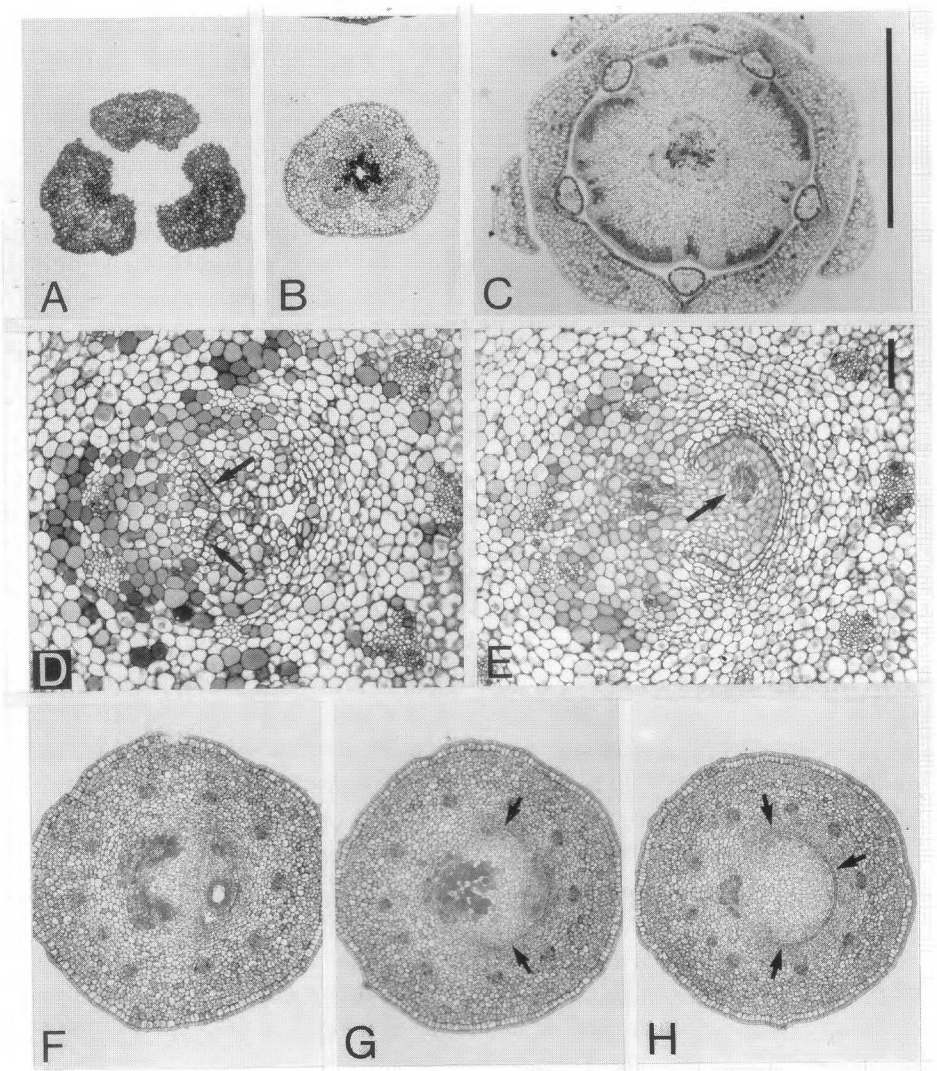


Fig. 5. Cross sections of the gynoecium of *Viburnum clemensae*. **A–C**, sections from above the ovary; A, stigma lobes; B, style; C, ovary roof nectary (note dark-stained nectar producing tissue in the peripheral regions and 3-parted vascular supply of style in the centre; also visible—from the centre outwards—staminodes, corolla, and free calyx lobes). **D–H**, ovary sections at different levels (as indicated in Fig. 6A); D, two aborted locules (arrows) and third, larger ("fertile") locule; E, placenta about to enter the locule, note that the vascular bundle (to supply the fertile ovule) is in an asymmetrical position (arrow); F, section through mid-ovule, showing embryo sac and vascular bundle; G, section through chalazal region, note size increase of placenta and somewhat semi-circular slit (arrows); H, lower third of ovary, note semi-circular slit (arrows) between enlarged placenta and ovary wall; in F–H, note the 10 peripheral vascular bundles and the bundle opposite the placenta (H) that starts splitting up at higher levels (G→F→E). A–H, microtome sections. Scale bars: 1 mm (A=B=C=F=G=H); 0.1 mm (D=E).

Fig. 5E shows a cross section in the region where the placenta enters the well-developed locule. In the placenta, the vascular bundle that supplies the fertile ovule is seen in an off-centre position. This is so because of the peculiar orientation of the anatropous ovule in the locule: the ovule is in a tangential position in relation to the entire ovary (cf. Fig. 6C), i.e., its micropyle neither points to the centre of the ovary nor away from it but sideways (consequently the vascular supply of the ovule—extending up to its chalazal region—is no longer exactly in the centre). This ovule orientation may be interpreted as being a remnant of the presumably "ancestral" situation in *Viburnum* (ovules *sideways* on each placenta, in two rows; cf. Wilkinson 1948: Fig. 11). Fig. 5F, an ovary section through roughly the middle of the ovule, also documents the ovule orientation: below, the sectioned embryo sac is visible and above, the vascular bundle running up to the chalazal region of the ovule.

The available preserved material was insufficient for detailed embryological work; it therefore remains unknown whether the species has an "*Allium*-" or "*Polygonum*-type" of embryo sac (both recorded for the genus; cf. Erbar 1994).

In her study of *Viburnum* ovaries, Wilkinson (1948) paid much attention to the vascularization of the ovary. The present investigation of *Viburnum clemensae* did not yield any significant differences to her findings: apart from the 10 bundles, in cross section forming a circle in the wall of the ovary (e.g., Fig. 5F–H), there is a solitary "central" bundle (left of the placenta in Fig. 5H) coming up from the base of the ovary. Higher up, this bundle splits into five (see Fig. 5G, F, E in sequence); one enters the placenta to continue into the fertile ovule ("large fertile ventral bundle" *sensu* Wilkinson 1948), the other four could be interpreted as a pair of "sterile ventral bundles" and "abortive ovular traces" (*sensu* Wilkinson 1948).

The presence of idioblasts filled with tannins or a tanniniferous substance (dark-stained areas in the depicted sections, e.g. Fig. 6A–B) is characteristic for all ovary tissues of *Viburnum clemensae*. The occurrence of tannin(-like) substances has already been mentioned by Wilkinson (1948) as being a common feature for the genus, but apparently they are not universally present (cf., for example, Erbar 1994: Fig. 37–38).

Fruits and Seeds

The fruits, crowned by the persistent calyx and the massive disk (Fig. 7A–C), are one-seeded ovoidal drupes, 9–12 × 6–8 mm in size. They are yellowish-green to yellow and ellipsoidal at first (Fig. 7A) and become orange-red to red and ovoidal at full maturity (Fig. 7B).

The solitary mature seed, *c.* 7 × 5.5 mm, fills up most of the interior of the fruit. It shows a distinct longitudinal furrow on the ventral (adaxial) side (Fig. 7D–F; see Seed Development and Anatomy, below, for explanations) and, moreover, strong ruminations ("folds") over its entire surface (Fig. 7G–H).

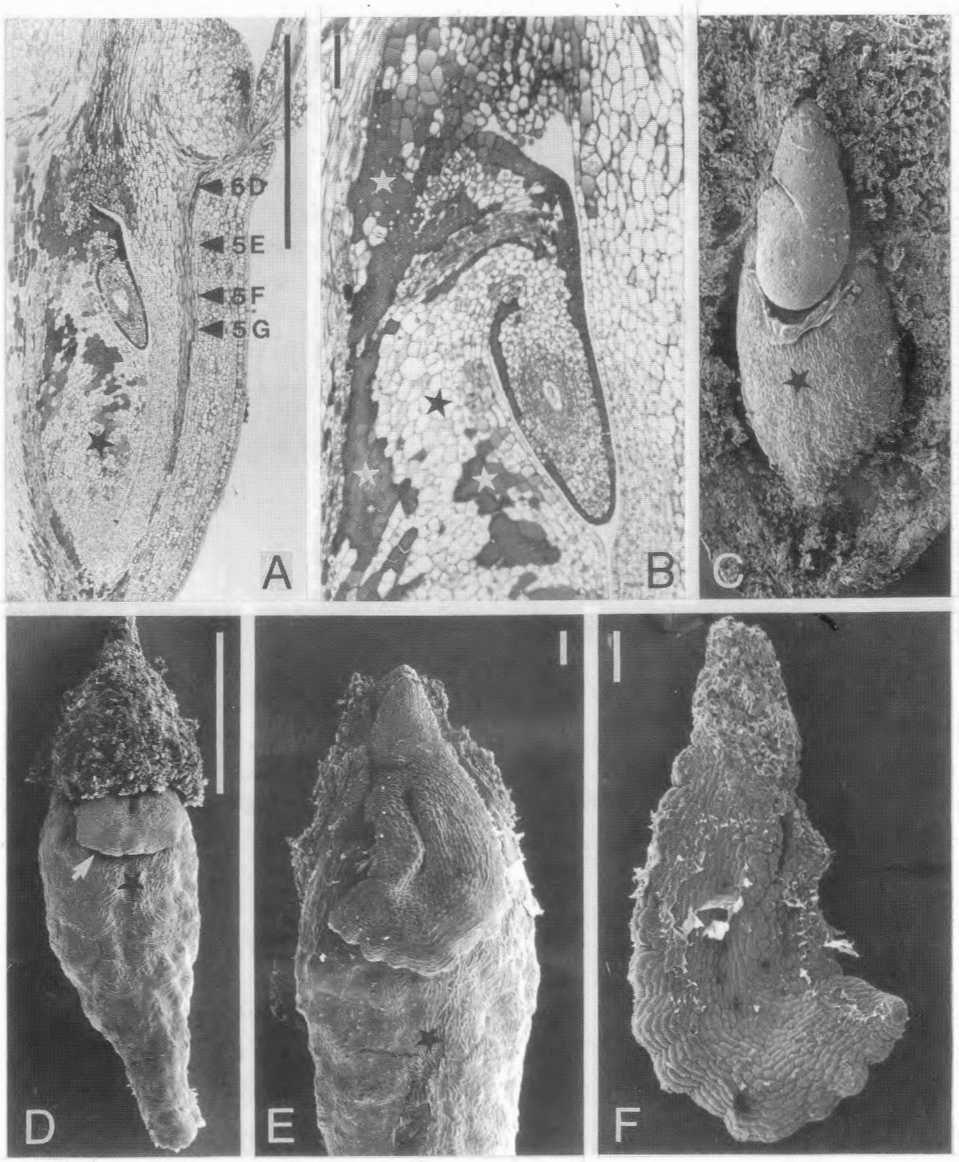


Fig. 6. Ovary, ovule and developing seed of *Viburnum clemensae*. **A–B**, longitudinal section of locule with ovule (B, detail of A); note enlarged placenta below ovule (★) (white asterisks: tannin-filled idioblasts); triangles indicate the planes of the sections reproduced in Fig. 5D–G. **C**, ovary wall removed to show ovule position and enlarged placenta (★) below ovule. **D–F**, developing seeds (surrounding tissues removed); D, very young seed (arrow) (above partially hidden by the developing endocarp) with enlarged placenta below (★); E, slightly older stage than D, note increased size of the developing seed in relation to the placenta (★) and the beginning rumination; F, adaxial side of developing seed (removed from D), note asymmetrical shape due to unequal development of rumination. A–B, microtome sections; C–F, SE-micrographs. Scale bars: 1 mm (A; D); 0.1 mm (B; C=E; F).

Fruit anatomy

The fruit wall is differentiated into an exocarp (fruit epidermis with a thick cuticle, Fig. 9B), a mesocarp of parenchymatic tissue and a several-layered sclerenchyma making up the endocarp (Fig. 9A). The mesocarp is rich in idioblasts filled with tannin (or a tannin-like substance) (Fig. 8, 9A–B) and, moreover, has idioblasts filled with crystal druses (Fig. 9C).

With regard to the endocarp, it is noteworthy that a preformed germination slit is present (as is known from other taxa with drupaceous fruits, e.g., numerous Rubiaceae: Robbrecht 1989), i.e., there is a distinct gap in the endocarp, located apically, in close proximity to the location of the embryo (Fig. 8F–G). The presence of this slit undoubtedly makes it easier for the radicle of the embryo to emerge from the seed.

Seed development and anatomy

Soon after fertilization, the former ovule starts enlarging and changes shape (Fig. 6D, compare with 6C). Already at very early stages of development, the seed starts showing ruminations, particularly in the chalazal region; this causes a very young developing seed to appear rather asymmetrical (Fig. 6E–F). In the stage depicted in Fig. 6E, the developing seed is still much smaller than the placenta, but this changes drastically later on.

During further development, the seed enlarges significantly and starts growing laterally around the placenta and eventually almost envelops it (Fig. 8A–E). This causes the characteristic longitudinal furrow on the adaxial side of a mature seed (Fig. 7E).

The exotesta of the seeds is one-layered, its cells do not show any secondary thickenings; at least in fully mature state, they are filled with tannins (Fig. 9D–F, compare with Fig. 9G). Below the exotesta, an endotesta layer is present; it is still distinct in immature seeds (Fig. 9G), but becomes quite crushed and is difficult to see in fully mature state (Fig. 9F).

The irregular seed surface is caused by the deeply and irregularly folded horny endosperm (ruminate endosperm) (Fig. 8A–E). The folds vary in extent and thickness (Fig. 9A), but there are always at least a few endosperm layers below the exo- (and endo-)testa (Fig. 9D).

The kind of rumination encountered in *Viburnum clemensae* corresponds to Periasamy's (1962) "*Spigelia*-type", which occurs—apart from Caprifoliaceae (*Viburnum foetens* was investigated by the author)—in taxa of the Araliaceae, Loganiaceae *s.l.*, Apocynaceae and Rubiaceae. It is characterized by "rumination preformed in the tissues of the seed coat" [as opposed to "unequal peripheral activity of the endosperm during later stages"] and an "only one layered mature seed coat".

At least for *Viburnum clemensae*, Corner's (1976: 88) statement that the endosperm [of *Viburnum*] is "subruminate from folds of the endocarp" does not hold. As can be seen from the sections (e.g. Fig. 8C–E, 9A), the endocarp is entirely smooth and "regular" and has nothing to do with the ruminations of the seed.

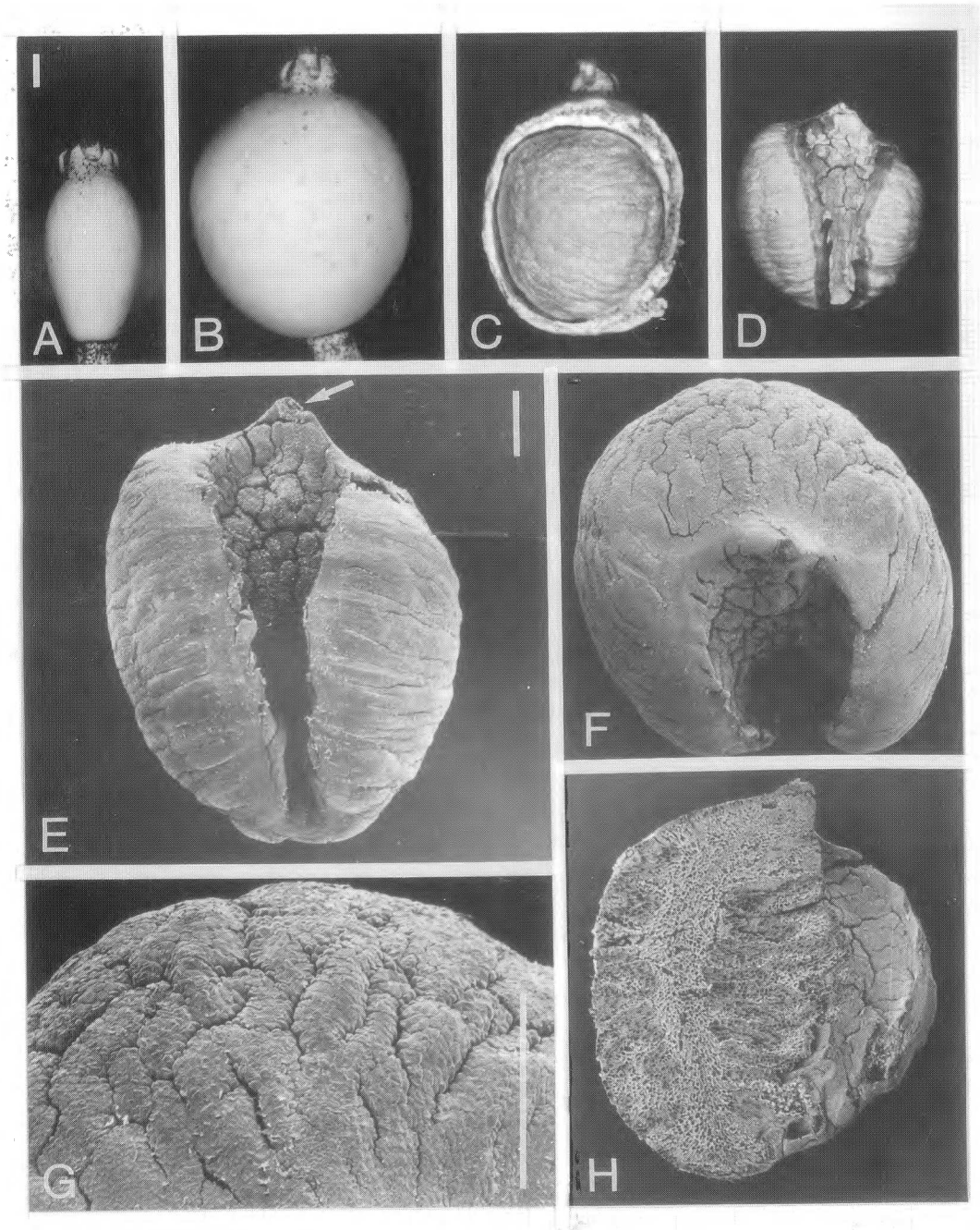


Fig. 7. Fruit and seed of *Viburnum clemensae*. **A**, young fruit. **B**, fully mature fruit. **C**, as B, but fruit wall removed to show abaxial side of seed. **D**, seed removed from C, view of adaxial side. **E**, as C; the arrow points to the area of the funicle. **F**, seed as seen from above. **G**, detail of seed surface, and **H**, longitudinal section of seed, both showing ruminations. A–D, LM; E–H, SE-micrographs. Scale bars: 1 mm (A=B=C=D; E=F=H; G).

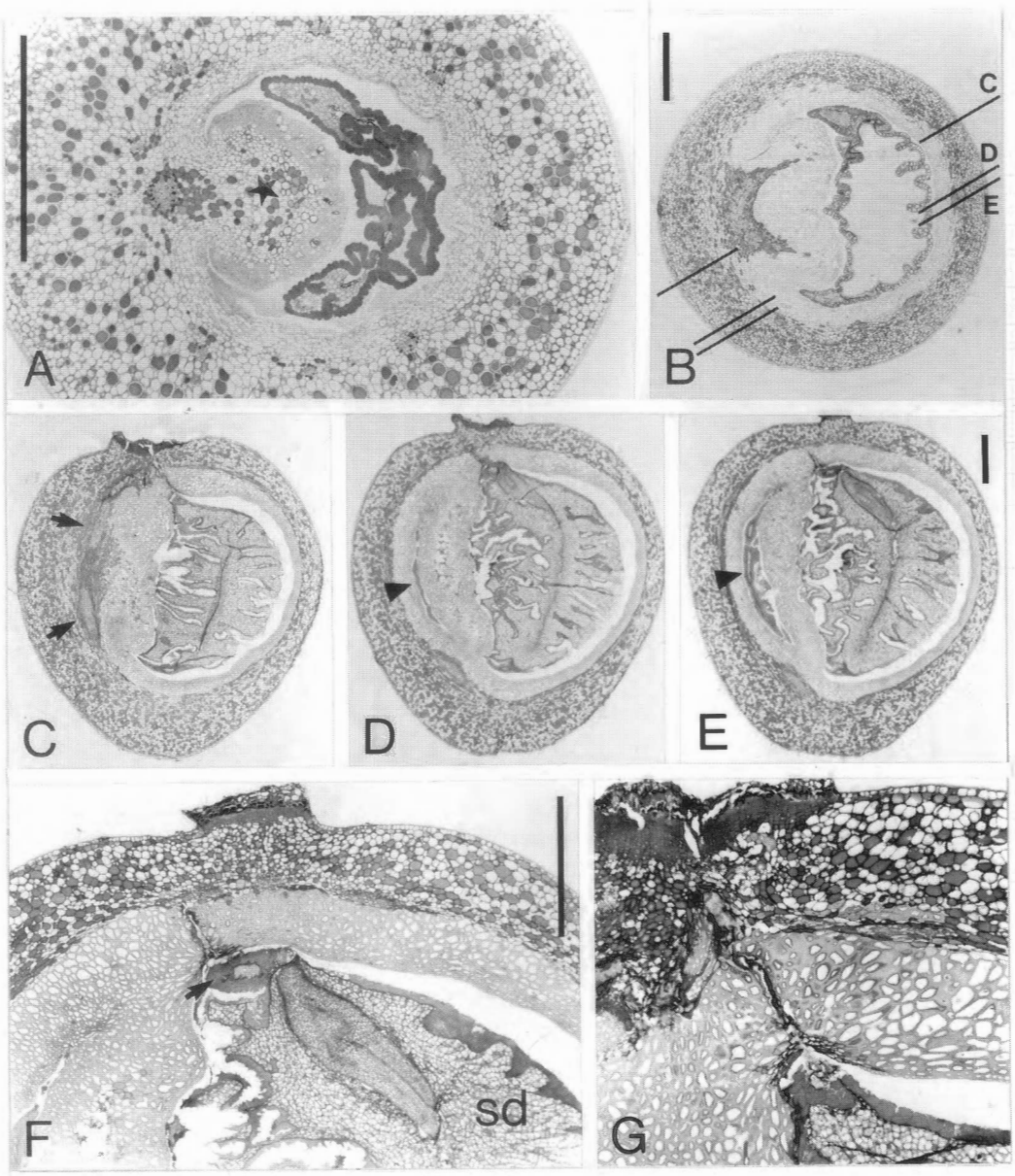


Fig. 8. Cross and longitudinal sections of fruit and seed of *Viburnum clemensae*. **A–B**, cross sections of immature (A) and nearly mature (B) fruit; note ruminate seed growing laterally around the enlarged placenta (★) and crescent-shaped locule. **C–E**, longitudinal sections in the planes indicated in B. C, note bundle (arrows) running opposite the placenta (compare with B); D–E, lateral extensions of the seed (triangles) show up to the left of the placenta. **F**, detail of apical part of sectioned fruit; note oblique, "apical" position of the embryo in the ruminated seed (sd) and area of the funicle (arrow). **G**, detail of fruit wall showing "apical" preformed germination slit in the sclerenchymatic endocarp. A–G, microtome sections. Scale bars: 1 mm (A=G; B; C–E; F).

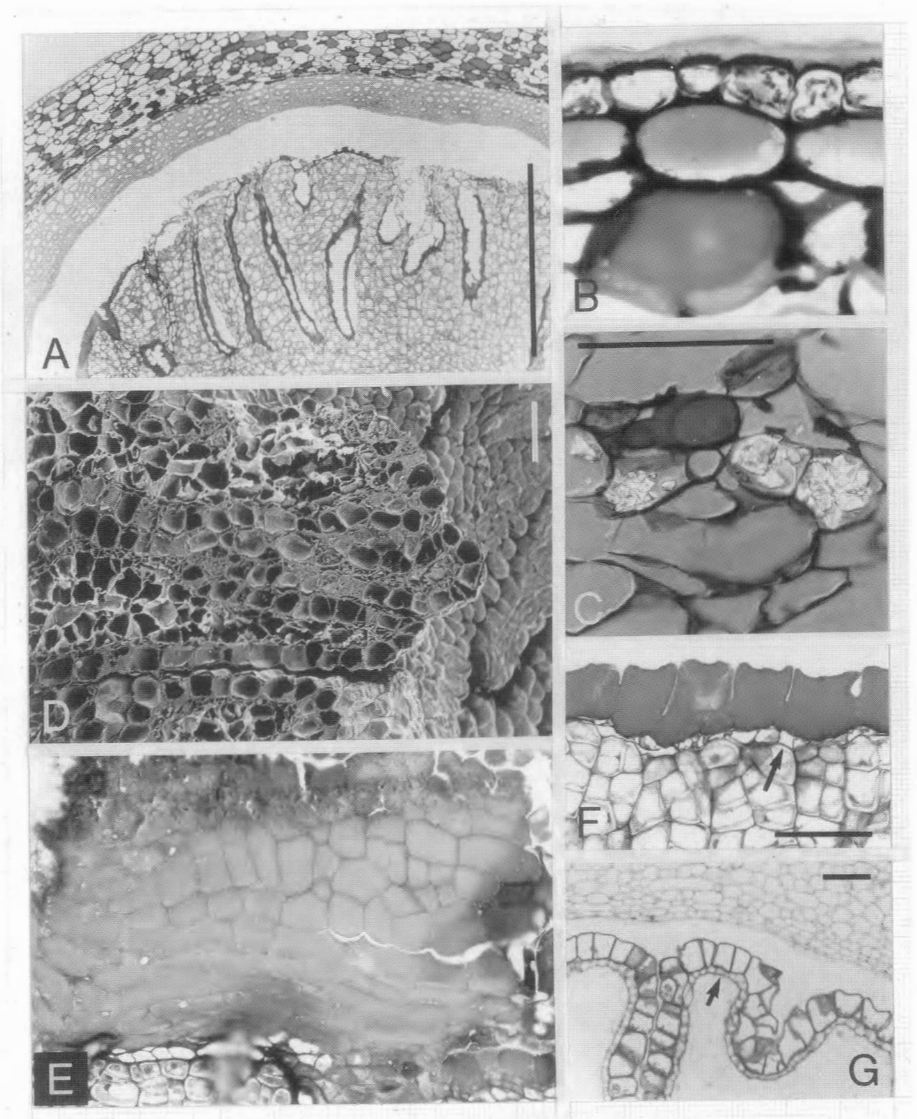


Fig. 9. Fruit wall and ruminated seed of *Viburnum clemensae*. **A**, portion of cross section of fruit and ruminated seed. **B**, outer portion of fruit wall: exocarp with cutinized outer epidermal walls, parenchymatic mesocarp with tannin-filled idioblasts. **C**, portion of the mesocarp showing idioblasts with crystal druses and tannins. **D**, ruminations ("folds") of the seed; dark coagulated contents seen in some of the exotesta cells are tannins. **E**, tangential section of a rumination "fold" showing dark-stained (tannin-filled) exotesta cells. **F**, cross section of tannin-filled exotesta cells, endotesta (arrow) and endosperm (below). **G**, cross section of portion of a seed from a not yet fully mature fruit; ruminations already present, but exotesta cells only partially filled with tannins (arrow: endotesta; seen above the seed: part of the endocarp, its cells not yet sclerenchymatic). A–C, E–G microtome sections (F, interference contrast); D, SE-micrograph. Scale bars: 1 mm (A); 0.1 mm (B=C; D; E=F; G).

Presumably caused by the formation of the ruminations that starts in the chalazal region (but later on spreading over the entire seed), the position of the embryo is no longer the same as that of the embryo sac in the ovule; it has been shifted to near the apex of the seed (and fruit), i.e., to a location nearly opposite the funicle, with the radicle pointing obliquely to it (Fig. 8F). The embryo is straight and small (*c.* 1.5 mm long), as is characteristic for the Caprifoliaceae (cf. Zomlefer 1994); radicle and cotyledons are of approximately the same length (Fig. 8F).

Pollen (Fig. 3H–J)

The pollen is spheroidal, small (20–22 µm in diameter) and 3-colpate. The exine is reticulate, with intraluminar bacula (lumina 0.25–0.5 µm in diameter). This agrees well with data for other *Viburnum* species (cf. Böhnke-Gütlein & Weberling 1981).

Distribution and Ecology

The species, previously thought to be endemic to the Mt. Kinabalu area in Ranau and Kundasang (cf. Kern 1951 and Kern & Steenis 1951), has also been recorded (Noorma Wati 1996) as being found in the Kota Belud, Tambunan and Tawau areas in Sabah. We collected it on Trus Madi, the second highest peak in Borneo after Kinabalu.

It grows on mountain slopes or ridges, both in primary and secondary forests and is recorded from altitudes ranging from 1300 to 2000 m.

SPECIMENS EXAMINED — ***Male flowering specimens:*** **BORNEO. SABAH:** Ranau, Upper Uniport Mile 38 1/4 (Sosopodon), *Mujin* SAN 36747 (SAN), mile 36 1/4 Ranau road, *Badak* SAN 32395 (SAN), Sosopodon, Jalan Lering, *Lajangah* SAN 33124 (SAN), Mt. Kinabalu, Mesilau River, *Chew & Corner* RSNB 4247 (SAN). Tambunan, Trus Madi range, logging road to Apin-Apin, *Sugau et al.* JBS 137 (SAN). — ***Female flowering specimens:*** **BORNEO. SABAH:** Tambunan, Trus Madi range, logging road to Apin-Apin, *Sugau et al.* JBS 134 (SAN, WU). — ***Fruiting specimens:*** **BORNEO. SABAH:** Ranau, Kundasang, N.P. Boundary, *Sadau* SAN 42473 (SAN), Sosopodon below Kinabalu, near Kundasang, *Mikil* SAN 46725 (SAN), above Kiau 11 Gurulau ridge near Kinabalu Nat. Park, *Kanis & Kurpin* SAN 53967 (SAN). Tambunan, Trus Madi F.R., above Sg. Kidukoruk, *Mikil* SAN 31770 (SAN).

Discussion

Our initial field identification of the investigated species as a member of the Rubiaceae (based on the characters given in the introduction) was undoubtedly wrong, although not fully unrealistic: Baillon (1880), for example, had suggested to merge Caprifoliaceae into Rubiaceae and, in the past, several genera have been transferred from Rubiaceae to

Caprifoliaceae (and *vice versa*) (see Kern & Steenis 1951) because certain character states are shared by both families.

Based on our present state of knowledge we can say with certainty that this presumed alliance cannot be upheld, and that the similar character states are the result of parallel evolution. The two families are not even in the same order. Nowadays, Rubiaceae are placed in the Gentianales, and Caprifoliaceae in the Dipsacales. As revealed by cladistic analyses (Donoghue 1983, Donoghue *et al.* 1992), the Caprifoliaceae are, however, polyphyletic. A position in the Dipsacales is only supported for 10 "core genera" (*Lonicera*, *Symphoricarpus*, etc.), whereas *Viburnum* and *Sambucus* belong elsewhere (Cornales?). An alliance to *Adoxa* (Adoxaceae) has been suggested and, based on cladistic studies, the cited authors suggest a placement of the two genera in the Adoxaceae, although this is not fully and generally accepted (cf. Erbar 1994); we, therefore, chose to leave *Viburnum clemensae* in "Caprifoliaceae *s.l.*".

The character states found in *Viburnum clemensae* are largely in agreement with those given for *Viburnum* in Donoghue's (1983) cladistic analysis, although there are some disagreements. Many character states (especially floral, fruit and seed features) can, however, not be directly compared because his data matrix was too limited (only a total of 13 characters covered).

Particularly noteworthy is the dioecy encountered in the investigated species. It seems to be a feature unique to *Viburnum clemensae*; we have been unable to find any report of its occurrence in literature, either for the genus or for the Caprifoliaceae *s.l.* as a whole. The species has paniculate, rather than umbel-like inflorescences (according to Donoghue the latter characterize the genus). The ovary position of *Viburnum* is given as "3/4 inferior" by Donoghue and other authors (because aborted locules and ovules are often found above the level of calyx and corolla insertion so that the ovary is no longer fully inferior), but this is definitely not applicable to *Viburnum clemensae*.

In summary, it seems that *Viburnum clemensae* is a rather unusual and aberrant species which, in appearance, is quite different from "typical" *Viburnum* species as they are found in Borneo.

ACKNOWLEDGEMENTS

Support of this study by the "*Fonds zur Förderung der Wissenschaftlichen Forschung*" (Project P10499-BIO) is gratefully acknowledged. Prof. B. Bremer (Uppsala University, Sweden) is thanked for running the DNA analyses and providing information on the investigated plant's correct identity, and Dr. K.M. Wong (Forest Research Centre, Sepilok) for critically reading the manuscript and valuable comments.